

Cradle Mountain National Park – an early part of the reserve system in Tasmania. (Photo by Esther Beaton.)

Manning *et al.*, 2004). Competing human demands and the extent of past impacts are almost always different in different places. Hence, there is *never* a set of identical candidate reserves from which to select (Prendergast *et al.*, 1999).

Political, economic and social factors *always* take precedence over ecological goals when land is considered for reserve allocation (Hunter, 1994; Pressey *et al.*, 1996; Lawton, 1997; Margules and Pressey, 2000). The tension between economic, social and ecological objectives makes reserve selection highly idiosyncratic. What is appropriate in one jurisdiction will be entirely unsuitable in others (Struhsaker *et al.*, 2005). For example, in the United Kingdom, reserve design is influenced by the fact that many reserves are acquired by different institutions, including government and voluntary bodies (Prendergast *et al.*, 1999).

In contrast, in many less developed nations, setting aside reserves without considering the interests, behaviour and attitudes of the local human population typically leads to conflicts and ultimately to degradation of the reserve (e.g. Western and Gichohi, 1993; Smith *et al.*, 1997; Harcourt and Parks, 2003; Struhsaker *et al.*, 2005). For example, Khirthar National Park is Pakistan's first and one of its most important national parks. It has several threatened species and some spectacular natural features, and it is also the home of almost 100 000 people who grow crops and graze animals there. These people are a critical element in all conservation strategies (e.g. Yamada *et al.*, 2004).

Successful reserve design is neatly illustrated by the example of Masoala National Park in Madagascar, where the design was based on a blend of ecological and socio-economic criteria, including strong local community and high-level political support (Kremen *et al.*, 1999) – the paper describing the design acknowledged the support of the US Ambassador and the President of Madagascar! Such idiosyncrasies are perhaps best summarised by Prendergast *et al.* (1999), who noted that: '*no single procedure for identifying areas of conservation interest is likely to be universally appropriate*'.

## 16.6 Island biogeography and the design of nature reserves

As noted previously in this chapter, large areas usually support more species than smaller ones (e.g. Arrhenius, 1921; Preston, 1962; Rosenzweig, 1995; see also Chapters 5 and 14). Species–area relationships are a pervasive feature of ecology (e.g. Newton, 1998; Fahrig, 2003). The theory of island biogeography (MacArthur and Wilson, 1963, 1967) was developed, in part, to explain the species–area phenomenon, particularly for island biotas. This theory was then extended by Diamond (1975) and many others (e.g. Terborgh, 1974; Diamond and May, 1976; Shafer, 1990), who likened oceanic islands to reserves and used the theory of island biogeography to develop generic design principles for protected areas. These principles were incorporated in the International Union for the Conservation of Nature's 1980 World Conservation Strategy (IUCN, 1980), and were recommended for use in guiding the management of wildlife populations in wood production forests (Davey, 1989b).

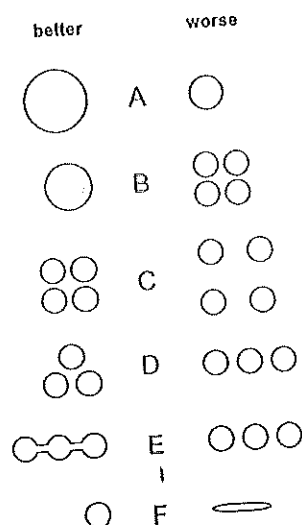


Figure 16.3. Principles for reserve design based on island biogeography theory (after Diamond, 1975).

Six general reserve design principles were derived largely from island biogeography theory (shown graphically in Figure 16.3):

- *Principle 1.* Large reserves are better than small reserves.
- *Principle 2.* A single large reserve is better than a group of small ones of equivalent total area (the basis for the so-called Single Large Or Several Small (SLOSS) debate).
- *Principle 3.* Reserves close together are better than reserves a long way apart.
- *Principle 4.* A compact cluster of reserves is better than a line of reserves.
- *Principle 5.* Circular reserves are better than long thin reserves.
- *Principle 6.* Reserves connected by a corridor are better than reserves not connected by a corridor.

#### Problems with the 'generic reserve design principles' derived from the island biogeography theory

The relationships between island biogeography theory and reserve design have been a highly controversial topic in conservation biology for several decades (see reviews by Gilbert, 1980; Burgman *et al.*, 1988; Simberloff, 1988; Shafer, 1990; Doak and Mills, 1994; Haila, 2002). There are many circumstances in which they do not hold, or in fact, their adoption could have an adverse effect on conservation values (Simberloff, 1988).

#### *Principle 1. Large reserves are better than smaller ones*

In general, larger reserves harbour more species, and all other things being equal, larger reserves are more effective for conservation than smaller ones. However, uncritical application of Principle 1 has led to excessive emphasis on large reserves (Lindenmayer and Franklin, 2002). Although large reserves are unquestionably important, small remnants can also have considerable value for biodiversity (Gascon, 1993; Powell and Björk, 1995; Turner, 1996; Palmer and Woinarski, 1999; McCoy and Mushinsky, 1999; Abensperg-Traun and Smith, 2000; Mac Nally and Horrocks, 2000). For example, Kirkpatrick and Gilfedder (1995) showed that small reserves, even those in poor condition, contained important populations of rare plants in otherwise extensively cleared parts of Tasmania. In other situations, larger reserves may not be appropriate. Studies of terrestrial gastropods in patches of remnant native vegetation in New Zealand showed that they were virtually confined to smaller habitat patches; smaller patches did not support the populations of feral Pigs that were a major predator of the snails (Ogle, 1987).

#### *Principle 2. A single large reserve is better than several smaller ones*

This principle has been discussed more than any other in the conservation biology literature over the past 30 years. The benefit of a large reserve compared with several smaller ones depends on:

- the typical size of disturbance events in the landscape
- spatial contagion in disturbance regimes (or the spatial extent of areas typically affected by the same catastrophic event, for example a high-intensity wildfire)
- spatial autocorrelation in year-to-year environmental fluctuations
- the dispersal capabilities of taxa targeted for conservation, that is, their ability to recolonise disturbed areas
- the demographics of populations in reserves.

If we ignore persistence and aim to maximise the number of species in reserves at the outset, then several reserves are likely to encompass a greater diversity of habitats and are therefore likely to harbour a greater number of species (see Kirkpatrick, 1994; Honnay *et al.*, 1999, for examples). A single reserve may be more susceptible to a single catastrophic event than a set of smaller, spatially separated ones (see Box 16.4). If a

## Box 16.4

## Reserve design for Leadbeater's Possum

Wood production activities and wildfires have important impacts on the distribution and abundance of Leadbeater's Possum (Macfarlane and Seebeck, 1991; Lindenmayer, 2000). The aim of management strategies is to conserve populations throughout the range of the species. How then should reserves be designed? Computer simulations were conducted for populations of animals in a nominal reserve area of 300 hectares, set aside as a single 300-hectare area,  $2 \times 50$ -hectare reserves,  $3 \times 100$ -hectare reserves and so on (Lindenmayer and Possingham, 1995). The probability of extinction was lowest for the set of intermediate-sized reserves ( $8 \times 50$ -hectare or  $6 \times 75$ -hectare patches; Figure 16.4). In scenarios where a single 300-hectare reserve was modelled, there was a high probability that the entire population would be eliminated in a single fire. Such risks were lower when the reserve system comprised several patches. These patches were sufficiently close that recolonisation of empty habitat was likely. Conversely, if the patches set aside were too small (e.g. 25 or 50 hectares), factors such as demographic stochasticity increased extinction risk. Thus, in the case of the design of reserves for Leadbeater's Possum, there is an important trade-off between the impacts of processes that influence very small populations at one extreme (demographic stochasticity) and the influence of fire regimes at the other. More recent work corroborated the need for several spatially separate reserves, but indicated that the size of individual reserves for Leadbeater's Possum should be larger than 75–100 hectares (McCarthy and Lindenmayer, 2000).

species has poor movement capabilities, then it is relatively unlikely to recolonise patches. In these cases, fewer larger reserves or a number of reserves located close together may be required, but at the cost of increased risk from correlated disturbance events and environmental variation.

The trade-off between large and small reserves only applies where the total area of a single large reserve is more or less equal to the total area of small reserves. A fragmented habitat that has several small patches contains a smaller (and a more extinction prone) total population than the original, non-fragmented habitat because the total area of habitat is reduced and the

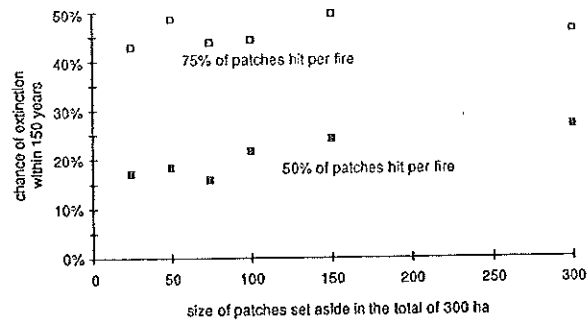


Figure 16.4. Reserve size, reserve number and extinction of Leadbeater's Possum.

movement of individuals (migration, dispersal) may be restricted (see Chapter 10). Furthermore, the resulting patches are generally no more independent of each other than they were before fragmentation (because they are at the same location in the environment), although fires or disease may spread more slowly, making fragments more independent than parts of a single large habitat.

*Principles 3 and 4. Reserves close together are better than reserves far apart and a compact cluster of reserves is better than a line of reserves*

Assertions that reserves close together are better than ones a long way apart, and that a compact cluster of reserves is better than a line of reserves (Figure 16.3) suffer from the same limitations as the issues outlined in the previous section. A lack of environmental correlation between habitat patches may mean that organisms can recolonise locally extinct patches more easily. Berger (1990), Murphy *et al.* (1990) and Stacey and Taper (1992) provide examples where a lack of environmental correlation between habitat patches or reserves benefited species persistence.

The best spatial arrangement of areas set aside for nature conservation will depend on the biology of the species at hand, the objectives of the reserve system and the management of the habitat around the reserves. It will be determined by the inter-play between correlations in environmental variation, disturbance regimes or catastrophic events, dispersal capability and the size and number of reserves.

*Principle 5. Circular reserves are better than long, thin ones*

The shape of reserves rarely receives much attention (Blouin and Connor, 1985). Circular reserves are considered to be superior to linear reserves because of

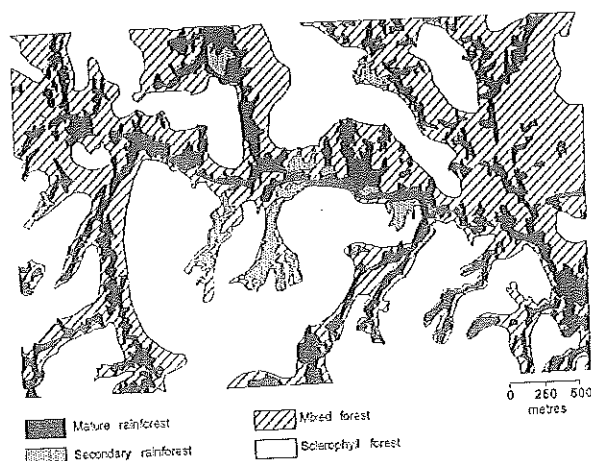
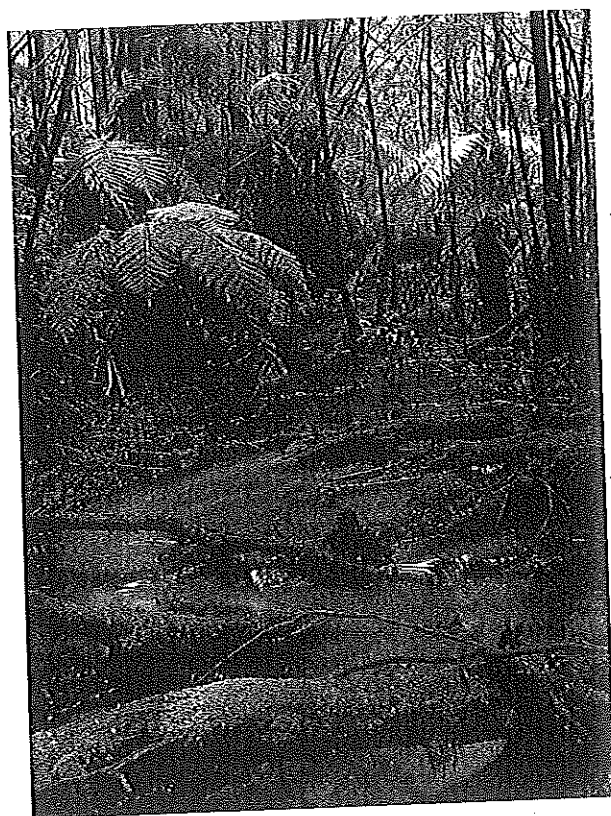


Figure 16.5. An example of the linear spatial arrangement of cool temperate rainforest patches in the O'Shannassy Catchment, Victoria (after Burgman and Ferguson, 1995).

the potential problems created by biotic and abiotic edge effects in linear reserves (see Chapter 10 on edge effects). For example, Reading *et al.* (1996) considered that round reserves would be better reintroduction sites than linear reserves for the Eastern Barred Bandicoot.



Linear riparian areas of cool temperate rainforest in the Central Highlands of Victoria. (Photo by David Lindenmayer.)

As with the other 'general reserve design principles', the issue should be considered carefully. Local context is likely to be more important than any generalisation. Linear reserves may encompass a larger range of habitat types and potentially more species. Configurations that conform with natural boundaries such as water catchments may be easier to manage, and landscape elements such as riparian vegetation may not be captured effectively by a circle. For example, cool temperate rainforests in Victoria (e.g. forests dominated by Myrtle Beech and Southern Sassafras) are largely associated with cool, moist riparian areas (Busby, 1986; Lindenmayer *et al.*, 2000a), and are characterised by linear spatial distribution patterns within larger areas of wet sclerophyll eucalypt forest (Figure 16.5). Similarly, relatively narrow linear reserves would effectively capture areas of wet sclerophyll forest adjacent to tropical rainforest in northern Queensland.

Circular reserves may also be more prone to degradation than linear reserves when the threat spreads from within a patch. For example, many vegetation types are associated with riparian environments, and the streams that run through their centre are a mode of transport for pathogens and weeds. In such cases, the larger the edge:area ratio, the slower will be the rate of loss of unaffected habitat.

*Principle 6. Reserves connected by a corridor are better than reserves not connected by a corridor.*

There has been considerable debate about the conservation value of wildlife corridors (Simberloff and Cox, 1987; Noss, 1987; Hobbs, 1992; Simberloff *et al.*, 1992; Bennett, 1998). Corridors may enhance the value of connected reserves in some instances. Chapter 10 discusses the advantages and disadvantages of corridors and highlights the fact that connected reserves may not always be better because the connections play a role in dispersal, and they affect the correlation of variation between environments in different patches (reviewed in Lindenmayer, 1998). Connections may be beneficial or detrimental to the persistence of species, depending on the species' biology and interactions with the environment (Lindenmayer and Franklin, 2002).

**Why island biogeography theory has limited applicability to reserve design**

The island biogeography theory treats reserves (and habitat patches) as 'isolated oceanic islands' and does not account for conditions and processes in surrounding



unreserved areas (Haila, 2002; Manning *et al.*, 2004). The theory ignores disturbance regimes, the magnitude and type of edge effects at reserve boundaries, and the suitability of surrounding unreserved areas for habitat and dispersal pathways, or as a source of invading species (Aldrich and Hamrick, 1998; Saurez *et al.*, 1998; Ås, 1999; Richetts, 2001). Therefore, the theory may fail where the surrounding area provides even temporarily suitable habitat (Zimmerman and Bierregaard, 1986), or when the importance of reserve size is outweighed by other factors, for example disturbance regimes, habitat conditions within and outside reserves (e.g. Fitzgibbon, 1997; Fox and Fox, 2000), heterogeneity and connectivity across landscapes (Brereton, 1997; Metzger, 1997), and the influx of organisms displaced from the adjacent unreserved areas (Bierregaard and Stouffer, 1997; Darveau *et al.*, 1995).

Island biogeography theory focuses on the numbers of species; however, in many reserve design cases, species diversity *per se* is not important. The number of species may increase (see Box 16.5) but large changes in species composition may be detrimental (Bennett, 1990b;

Hutchings, 1991, in Gascon and Lovejoy, 1998). Rather than the number of species, reserve design is concerned with biotic composition, the identity of taxa in reserve systems (Murphy, 1989; Doak and Mills, 1994), the viability of populations (Grumbine, 1990; Lamberson *et al.*, 1994; Gurd *et al.*, 2001), and the need to optimise representativeness or comprehensiveness (Mackey *et al.*, 1988; Scott *et al.*, 1993, 2001).

### Summary: Island biogeography theory and reserve design

Zimmerman and Bierregaard (1986), Burgman *et al.* (1988) and Doak and Mills (1994) showed why island biogeography theory often has little practical value in reserve design. Reserves are not isolated oceanic islands (Saunders *et al.*, 1991; Haila, 2002). Attributes of and processes in surrounding unreserved land are important (Gascon *et al.*, 1999), and species diversity alone is not sufficient for reserve selection. Rarely are there two or more ecologically similar areas from which to choose (Simberloff, 1988; Larsen, 1994). On this basis, Lindenmayer and Franklin (2002) argued that it is better to design reserves to satisfy specific objectives rather than apply general design principles from island biogeography theory.

Despite the clear limitations of island biogeography theory, it has had a major impact on the evolution of conservation biology, because of the considerable effort dedicated to testing its predictions (see for example, Shafer, 1990). Testing and falsifying theory is a critical part of the scientific process. Indeed, in the preface of their seminal book, *The Theory of Island Biogeography*, MacArthur and Wilson (1967, p. v) noted that:

*We do not seriously believe that the particular formulations advanced in the chapters to follow will fit for very long the exacting results of future empirical investigation. We hope instead that they will contribute to the stimulation of new forms of theoretical and empirical studies, which will lead to stronger general theory.*

### Box 16.5

#### Empirical examples of the shortcomings of island biogeography theory

One of the general rules of reserve design derived from island biogeography theory is that smaller patches created by habitat fragmentation support fewer species. Natural resource management and conservation require simple rules to guide decisions. However, simple and general 'rules' are nearly always wrong in some circumstances. The Biological Dynamics of Forest Fragments Project in Brazil found that edge effects and matrix conditions were key factors and that their impacts were substantially more important than fragment size for some animals (Brown and Hutchings, 1997). In that study, there was an increase in frog, small mammal, and butterfly species richness following the isolation of rainforest patches, which was contrary to predictions based on island biogeography theory (Gascon and Lovejoy, 1998). Species richness was elevated by an influx of taxa capable of using the changed matrix. Estades and Temple (1999) similarly recorded increased bird species richness in small rather than large Southern Beech (*Nothofagus* spp.) forest remnants embedded within an exotic Radiata Pine plantation in Chile.

### 16.7 Conclusions

Protected areas serve the needs of both species and ecosystem conservation, and they are a core component of conservation strategies worldwide. It is tempting to think that a reserve system will guarantee the persistence of the biodiversity of a region, but this notion is naive. Reserves are one of the most important